

TAXONOMIC AND CYTOLOGICAL RELATIONSHIPS OF YUCCA AND AGAVE

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With plate 55

The senior author, during the past two years, has made an extensive study of *Yucca* and related genera. These genera have been collected from western Texas, New Mexico, Arizona, and the southern areas in California, Nevada, Utah and Colorado. The distance covered in this area has approximated 25,000 miles, and no day of travel passed without encountering numerous species of these plants.

Identification of *Yucca* species in the field has been difficult because of the extreme variability of all species, and the overlapping range of two or more similar species. For example, in the group of filiferous-leaved *Yuccas* with dehiscent fruit, the leaf characters have at times been used as a basis for species differentiation, but as a practical guide in the field these characters are often unreliable and confusing. On a single inflorescence the flowers vary little in size and form, but two inflorescences from adjoining plants, apparently of the same species, may differ in habit; the flowers may differ in shape and size of corolla-segments, ovary and style; and vary in length, form and pubescence of filaments. Among the fleshy-fruited *Yuccas*, one species seems to have two distinct forms; one with a vigorous fleshy inflorescence and large flowers, and the other with a compact, more ligneous inflorescence and more numerous small flowers.

In regions where closely allied species occur, their separation in the field is extremely difficult. Within the range attributed to *Y. angustissima* are plants of vigorous growth quite different than the expected type. In some respects, they resemble *Y. glauca* whose range is supposed to begin hundreds of miles further east. At the point of worst confusion has one encountered intermediate segregates from species hybrids, or are different types variants of a single species?

In most respects the allied genera *Clistoyucca*, *Hesperoyucca* and *Samuela*, separated by Trelease (1902), are similar to *Yucca*. *Yucca* and *Agave* are also similar in various striking details although these genera are placed in different families by most taxonomists.

The occurrence of transitional forms of *Yucca* species and the similarity of closely, and even distantly related genera, has led to a cytological study of these plants in order to compare their chromosome number and morphology. Material was collected in the field by the senior

author. Flower buds at different stages of development were fixed in a mixture of acetic acid and alcohol, and later transferred to 70 percent alcohol. Chromosome counts were obtained from aceto-carminic smears by the junior author.

Permanent smears were also made from pollen mother cells of *Agave americana* collected at the Bermuda Biological Station, from *Agave virginica* from the Missouri Botanical Garden, and from *Yucca flaccida* and *Y. filamentosa* grown in the Arnold Arboretum.

The chromosomes of *Yucca flaccida* have been described in detail by O'Mara (1931). At the first meiotic division there are 5 pairs of long chromosomes and 25 pairs of very small chromosomes. The long chromosomes have an average chiasma frequency of 3 per bivalent at metaphase, while each small bivalent has only a single terminal chiasma. The pairing is very regular and lagging univalents or other abnormalities were not observed. The extreme differences in chromosome size and the large number of chromosomes is rather unusual in the plant kingdom.

All of the species of *Yucca* examined have the same chromosome constitution. These include *Y. flaccida*, *Y. filamentosa*, *Y. elata*, *Y. constricta*, *Y. rupicola*, *Y. macrocarpa*, and *Y. angustissima*. The chromosomes of *Y. flaccida* and *Y. filamentosa* are shown at different stages of meiosis (figures 1, 2, and 3). The five pairs of large chromosomes are conspicuous at all stages. There is considerable variation in the size of the 25 small chromosomes, but all are relatively small.

The closely related genera examined also have exactly the same chromosome constitution as *Yucca*. These include *Hesperoyucca Whipplei*, *Hesperaloe parviflora*, and *Samuela Faxoniana*. Unfortunately, favorable material was not obtained from the related genera *Nolina* and *Dasylirion*. Counts from somatic cells of *Nolina* show that there are about 38 chromosomes which differ considerably in size, and most, if not all, of those chromosomes have median or sub-median spindle fiber constrictions. The more distantly related genus *Dracaena* (*D. arborea*) also has about 38 somatic chromosomes.

The species of *Agave* studied have 5 pairs of large chromosomes and 25 pairs of small chromosomes. The chromosomes of *A. virginica* and of *A. americana* are shown at different stages of the first meiotic division (figures 4, 5, and 6). Aceto-carminic smears of *Agave consociata* also show the same chromosome number and morphology. According to Mr. S. Horovitz of the University of Buenos Aires, *Agave filifera* also has 5 large and 25 small pairs of chromosomes.

The Agavoideae include according to Engler and Prantl the genera

Agave, *Polianthes*, *Bravoa*, *Furcraea* (*Fourcroya*) and *Beschorneria*, all natives of central America, and the Australian genus *Doryanthes*. According to Heitz (1926) *Furcraea altissima* has 10 large somatic chromosomes and about 40 small ones while *F. Lindeni* has 10 large chromosomes but only 30 small ones. We have found 10 large chromosomes and 50 small ones in aceto-carminic preparations of root tips from *Furcraea Bedinghousii*, but in order to get satisfactory preparations it was necessary to isolate single dividing cells and flatten the metaphase chromosomes by heat and slight pressure. According to Heitz, Müller's work on *Beschorneria* shows chromosome numbers similar to those of *Furcraea*.

As a rule pollen grain size is generally correlated with chromosome number in closely related species. The size and morphology of the pollen grains appear to be very similar in the following species;—*Yucca macrocarpa*, *Y. Treculeana*, *Y. baccata*, *Y. elata*, *Y. Reverchoni*, *Y. Thompsoniana*, *Y. mohavensis*, *Clistoyucca brevifolia*, *Hesperaloe parviflora*, *Hesperoyucca Whipplei*, *Agave Havardiana* and several unidentified species or varieties of *Yucca* and *Agave*. Each species and variety examined had almost 100 percent of morphologically perfect pollen grains.

DISCUSSION

The confusing variation within species and the intermediate forms of *Yucca* might be interpreted as the result of extensive hybridization between species and varieties. All of the species examined show regular chromosome behavior at meiosis and practically all of the pollen is morphologically perfect. If the questionable forms are hybrids the parental varieties or species must be closely related and possess very similar genomes. In respect to chromosome number and chromosome morphology all of the species studied seem to be very similar. If the chromosomes of different species are compatible with each other, a considerable amount of crossing might be expected and would be limited only by geographic isolation and differences in time of flowering. The cytological analysis alone offers little help in solving the cause of variations within and between species of *Yucca*.

The striking similarity of the chromosomes of *Yucca* and *Agave* and their allied genera indicates a close relationship between these two groups, even though they are referred to different families. The chromosome constitution, 5 pairs of large chromosomes and 25 pairs of small chromosomes, is so unusual that it cannot be due to chance. The two genera are also similar in many taxonomic characters. A brief comparison of the two genera, and of the families to which they

belong, has been prepared by Dr. Ivan M. Johnston of the Arnold Arboretum, and is quoted below.

"*Yucca* belongs to the Liliaceae and *Agave* to the Amaryllidaceae. The Amaryllidaceae, having an inferior rather than a superior ovary, are evidently more specialized in basic floral structure. Taken as a whole the two families differ only in this character of the ovary. There is every evidence that the Amaryllidaceae have been derived from the Liliaceae and there are some very good reasons to suspect that the former are a polyphyletic group with the several points of origin in the Liliaceae.

Yucca and *Agave* are similar in many striking details. Both are coarse fibrous perennials with usually firm, long-enduring, monocarpic leaf-rosettes that are not common in their families. The large panicles are similar in basic structure and pattern.

Yucca has a superior ovary; the filaments are attached at the base of the corolla, bearing small firmly affixed anthers which do not surpass the corolla-lobes.

Agave has an inferior ovary; the stamens are attached in the corolla throat, the linear filaments bear large linear versatile anthers usually protruding beyond the corolla-lobes.

While *Yucca* is more simple than *Agave* in structure of ovary, and presumably belongs to a generally more primitive family, its staminal structures and the complex symbiotic relation required in its pollination are distinctly far in advance over conditions found in *Agave*. It is evident, therefore, that *Agave* could scarcely have been evolved from *Yucca* (including *Samuela*, *Hesperoyucca*, *Cleistoyucca* and *Hesperaloe*) as now constituted.

Yucca is generally accepted as having relations in *Nolina*, *Dasyllirion* and *Dracaena* of the Liliaceae. *Furcraea*, in the Amaryllidaceae, is a relative of *Agave* although it possesses many important details of habit and floral structure very similar to those found in the relatives of *Yucca*. If *Yucca* is a reasonably close relative of *Agave*, as I believe it is, then it is probable that the affinity is to be traced through the related genera mentioned."

In the Dracaenoideae only the Yuceae have 5 large and 25 small pairs of chromosomes. All of these chromosomes have terminal spindle fiber attachments. In the two species examined (*Nolina* sp. and *Dracaena arborea*) in the Nolineae and Dracaeneae the somatic chromosome number seems to be about 38. These chromosomes do show considerable size differences but not as extreme as in *Yucca*, and the spindle fiber attachment constrictions seem to be median.

In the Agavoideae the two genera studied, *Agave* and *Furcraea*, have

chromosomes very similar to those of *Yucca*. The cytological comparison shows a very close relationship between the Yuccaceae and certain genera of the Agavoideae, but *Nolina* and *Dracaena* do not seem to be the connecting link between these groups.

According to Engler and Prantl, all genera of the Yuccaceae, and with the exception of the Australian genus *Doryanthes*, all genera of the Agavoideae, are natives of Central America. These genera are closely related as indicated by both taxonomic and cytological characteristics. It is of interest to note that the African Aloinae, including the genera *Aloe*, *Gasteria*, *Apicra* and *Haworthia*, are in some respects similar to the *Yucca*-*Agave* group. All of these African genera have the same chromosome number, and the chromosome complex includes both large and small chromosomes. There are 4 pairs of large chromosomes and 3 small ones in each of these genera (Gaiser, 1930). The morphological characters and the similarity in size differentiation of the chromosomes seems to indicate a remote affinity between the Aloinae of the Old World and the *Yucca*-*Agave* group of the New World.

SUMMARY

Yucca and *Agave* are similar in many taxonomic characters although one genus is placed in the Liliaceae and the other in the Amaryllidaceae. *Yucca* and the closely allied genera *Hesperoyucca*, *Hesperaloe*, and *Samuela*, have 5 pairs of large chromosomes and 25 pairs of small chromosomes at the meiotic divisions. Exactly the same chromosomes constitution is found in *Agave* and in at least one species of the closely related genus *Furcraea*. The similarity in taxonomic characters and chromosome constitution indicates that these genera have had a common origin and are closely related.

The variability within and between species of *Yucca* is not correlated with any variation in chromosome number or irregularity in chromosome behavior.

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